CAUSES OF STERILITY IN WHEAT

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ENVIRONMENTAL FACTORS AFFECTING BORON DEFICIENCY

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Abstract

Boron deficiency interacts strongly with environmental factors. Whilst the mechanisms governing these interactions are poorly understood, they stem from the need for a continuous supply of B to growing tissues in the plant. Boron deficiency occurs when the rate of supply of B to growing tissues falls below the rate of demand. It can occur when demand increases as a result of increased absolute growth rate or as internal requirements increase to cope with environmental stresses such as high light intensity or low temperature. Supply may be depressed by environmental factors such as low soil water and low temperature which depress B uptake by roots. That these factors act in a dynamic rather than a static manner adds to the challenge of predicting when and where B deficiency will occur and its impact on seed yield in wheat crops.

INTRODUCTION

Clear proof that boron (B) is an essential element for plant growth stems back to 1923 but since then our knowledge of B has remained at a fairly descriptive level: B is know more for the consequences of its deficiency in the field and in artificial media than for its cellular function. Research for most of the last 70 years has been hampered by the lack of sensitive analytical techniques for B detection in plant cells and organelles. That may be about to change with some research groups now applying new techniques such as B^{10} and B^{11} enrichment ratios (measured by ICP-MS) to directly test several of the key assumptions about the function and partitioning of B in plants and plant cells (eg. Brown and Hu 1993).

Boron nutrition has been recently reviewed by Romheld and Marschner (1991) who examined its function, by Moraghan and Mascagni (1991) who reviewed environmental factors affecting its availability, and by Shorrocks (1991) who edited the proceedings of a workshop on B held in 1990 which discussed its behaviour, function and significance in agriculture.

In brief, the key characteristics of B in plants are:

1. most plant B is strongly associated with cell walls (Matoh *et al.* 1992).

2. cellular functions of B are most likely those associated with the cell wall, and at the plasmalemma - cell wall interface (Loomis and Durst 1993).

3. B uptake by roots and its transport in shoots is predominantly a passive process mediated by water transport within the plant.

4. B is mobile in the xylem of plants but for most practical purposes can be considered phloem immobile, ie. negligible B incorporated into tissues following uptake by the roots can be remobilized and retranslocated to other parts of the plant even when external supply is limited. This point is contested by some research notably that by Shelp and colleagues (Shelp 1993).

5. a continuous supply of B is required from the soil to growing parts of plants to avoid B limitations on growth.

6. factors which hinder B uptake, water uptake, or water flux to growing parts relative to the demand for B in growing tissues may induce B deficiency.

The paper therefore will focus on environmental factors affecting B deficiency particularly those that might induce wheat sterility by inducing B deficiency. Boron requirements of plants can be divided into three discrete components, each of which is subject to different environmental influences.

1. Environmental factors affecting the internal requirements of plants for B. This concerns the concentrations needed in growing plants parts for their function. Internal B requirements might differ for example between roots and shoots, among leaves, stems, flowers, and fruits, and within these plants parts at different stages of their development.

2. Environmental factors affecting the external requirements of plants for B. This concerns the boron supply characteristics of soils so that the rate of flux of B into the plant is sufficient to meet demands for growth.

3. Environmental factors affecting the total requirements for B which is the amount in total that must be taken up by the crop during the growing season: it may vary from site to site according to the growth potential of the crop, and during the growing season of a single crop.

INTERNAL REQUIREMENTS

1. LIGHT

The best evidence to date that light may affect internal B requirements of plants is from the study of Noppakoonwong *et al.* (1993). In that study, black gram was grown in a glasshouse with adequate or deficient levels of B in solution until emergence of the first trifoliate leaf after which half of the plants were shaded decreasing light intensity from 70% to 30% of full sunlight. Shading decreased the leaf B concentration required for unrestricted leaf expansion from 15 to 10 mg B/kg dry matter. Previous studies had also suggested that increasing light increased internal B requirements of plants but these studies were less definitive than Noppakoonwong *et al* . (1993) because they either used unrealistically low light intensities, or confounded effects of light on growth with effects on internal requirements, or failed to distinguish between internal and external B requirements.

According to Shorrocks (1991), the fact that phenol synthesis is stimulated under high light represents a possible physiological basis for an increased B requirement. Boron in cells complexes with phenols causing them to polymerize and in most circumstances systhesize lignin. By contrast, under B deficiency, phenols may accumulate generating oxygen free radicles which are toxic to plant membranes. Thus, under high light, the cellular B requirement may increase in order to maintain membrane function. However, a causal relationship between high light, increased phenols and increased B requirements remains to be demonstrated. Indeed, from the data of Noppakoonwong *et al.* (1993) it is not even possible to be sure that increased light intensity as opposed to increased radiant energy was the cause of the increased B requirements for leaf expansion. For the present project, a close examination of available data on changes in light intensity during the growing season of sub-tropical wheat warrants attention. Further discussion is needed on how to use the radiation data being collected to quantify changes in light intensity. Light intensities during the stages of reproductive development most likely to affect wheat sterility are of particular interest.

2. TEMPERATURE

Several reports appear in the literature linking low temperature damage in plants and B deficiency (Shorrocks 1991). The substance of these reports is limited to observations of increased frost or low temperature damage in shoots when plant B status is low, and in some cases, alleviation of the injury with foliar B sprays. Experimental evidence that low temperatures increase sensitivity to B deficiency is limited to one brief report by Parr and Loughman (1983). Parr and Loughman (1983) examined the response of P uptake by *Zea mays* to decreasing temperature in the presence or absence of B in solution. In solutions supplied with B, the uptake of P declined with decreasing temperature but below 20 °C there was a distinct inflexion in the curve implying a temperature dependent change in membrane conformation from a fluid to a gel state. That low temperature causes a change in membrane properties has been reported previously (Lyons and Raison 1970). What had not been previously reported was the findings of Parr and Loughman (1983) that the critical temperature at which membrane properties changed, depressing P uptake, was 2 °C higher in B deficient solutions than in B adequate solutions. These results, limited though they are, imply that the low B tissues might be more sensitive to cold temperature damage to membranes than B adequate tissues.

In 1994, at Tonglu in Zhejiang province, we observed that oilseed rape plants exhibited foliar symptoms indicative of frost damage. The symptoms were observed in late March some 10-

14 days after snow falls which remained on the ground for 2 days. It was only in plots without B fertiliser that frost damage occurred in leaves: those treated with B fertiliser at sowing were free of the symptoms. Thus it appears that leaf tissue of oilseed rape was more sensitive to frost damage when low in B. However, the converse, that low temperature increases internal B requirements has not been demonstrated.

Interesting as these observations are, their relationship to B deficiency and to internal B requirements is not clear. Temperatures to which winter rape is exposed in China vary both temporally and spatially. For example, at Hangzhou minimum temperatures in December and January in 1993 were appreciably lower than the same months in 1994, but by contrast, minimum March temperatures in 1994 were lower. Temperature minima in 1991, 1992, 1993, and 1994 were -8.4, -3.4, -6.2 and -3 °C, respectively. Episodic low temperature events could be the cause of site-to-site and year-to-year variation in internal B requirements of oilseed rape, and therefore in pod set. For example, the much lower percentage seedling mortality after transplanting into low B soils in 1993 than in 1992 in an experiment at Tonglu was the opposite of what would have been expected from the difference in soil B levels but may be associated with the generally higher temperatures from November 1993 to February in 1994.

Further studies to establish a meaningful causal linkage between low temperature damage and plant B status would be particularly useful. Controlled environment studies would appear to be necessary to establish such a linkage. However, field demonstration of the significance of a low temperature effect is also necessary and might come from carefully instrumented sites where detailed diurnal records of soil and air temperature are available and where simple transparent plastic canopies are constructed over plants to raise air temperatures during critical stages of crop development.

EXTERNAL BORON REQUIREMENTS

1. SOIL WATER

Boron deficiency is most common in seasons of below normal rainfall (Moraghan and Mascagni 1991; Shorrocks 1991). As B uptake is a passive process that depends on the movement of B in the transpiration stream, decreases in water uptake that occur in dry soils are expected to depress B uptake. Moreover, the uptake of B fertilizer from surface soil layers is very poor when the surface soil dries out (Hobbs and Bertramson 1949). However, Shorrocks (personal communication) points out that high light intensity probably also occurs in seasons of below normal rainfall so that the conclusion that low soil water induces B deficiency in drier than normal seasons cannot be unequivocably deduced.

Noppakoonwong (1993) showed that in B fertilized soils, the concentration of B in recently matured leaves of black gram was increased with increasing soil water content (Figs. 1,2). She also showed that leaf B concentrations which declined sharply as soil water levels declined, increased rapidly following rainfall (Fig. 1). Thus soil B uptake responds dynamically during a growing season in response to changes in soil water supply. Periods of low soil water content which coincide with critical phases of reproductive growth may be critically important for sterility in wheat.

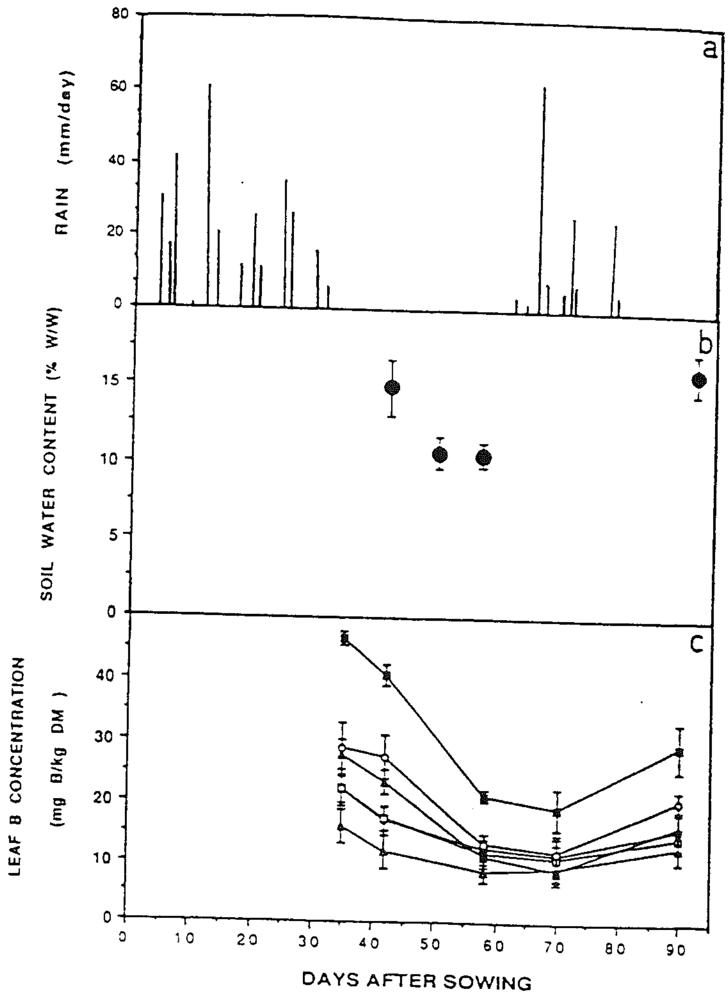
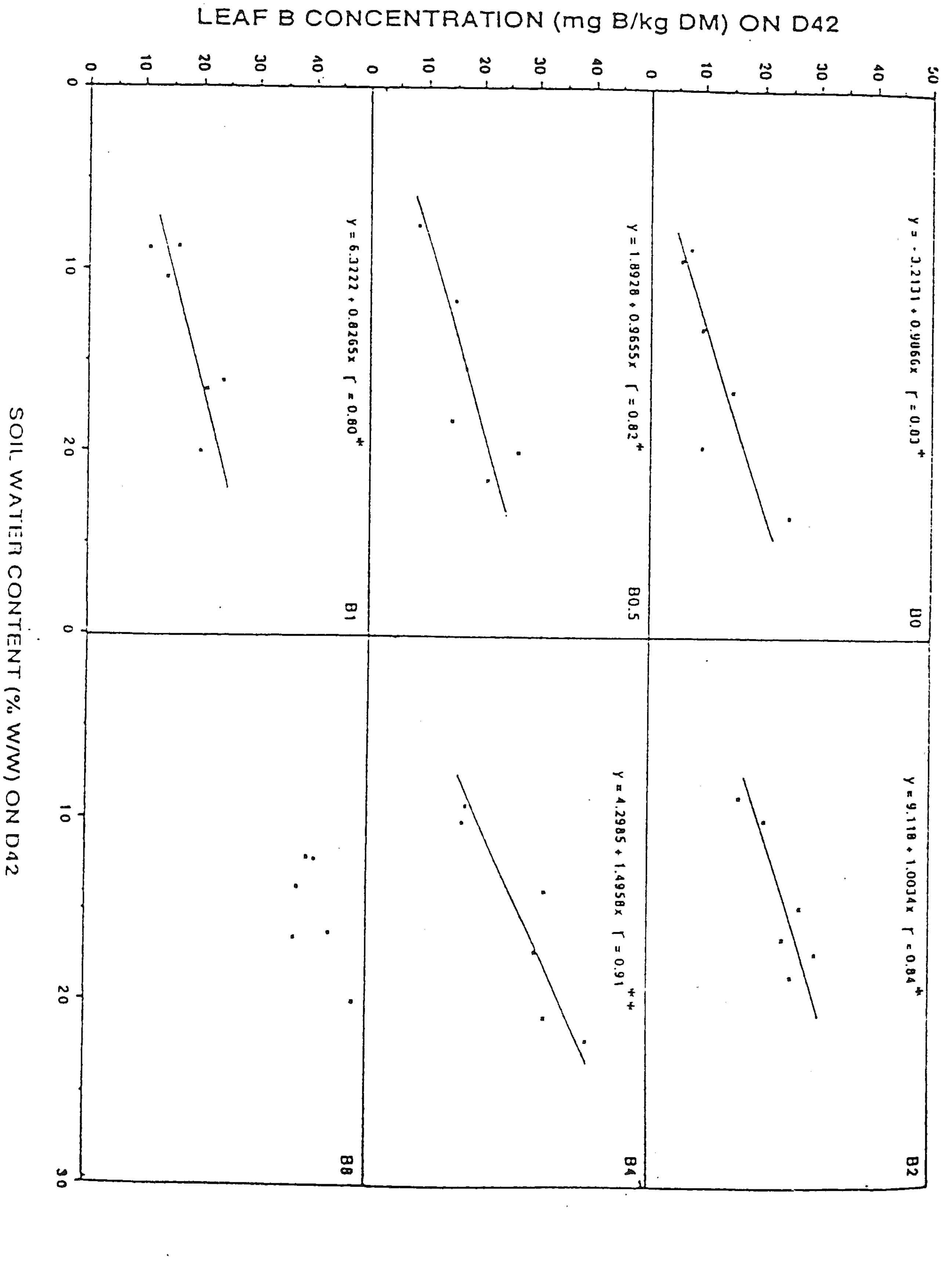


Figure 1. Relationship between rain events, soil water content and leaf B concentration in the youngest fully expanded leaf of black gram grown in Chiang Mai, Thailand. Source: Noppakoonwong (1991).


LEAF B CONCENTRATION (mg B/kg DM) ON D42
SOIL WATER CONTENT (% W/W) ON D42
y = -3.2131 + 0.9066x r = 0.83
B0
y = 9.118 + 1.0034x r = 0.84
B2
y = 1.8928 + 0.9655x r = 0.82
B0.5
y = 4.2985 + 1.4958x r = 0.91
B4
y = 6.3222 + 0.8265x r = 0.80
B1
B8

At the other end of the spectrum, low vapour pressure deficits in the atmosphere may also be the cause of restricted B uptake into growing plant parts. That B uptake and transport to plant parts occurs largely through xylem supply, and that xylem supply in turn depends on transpirational losses of water from that plant part suggests a close linkage between B deficiency and atmospheric vapour pressure deficits. Little appears to have been reported on this association of B deficiency with vapour pressure deficits. It does warrant attention in the present study on wheat sterility.

2. SOIL TEMPERATURE

The significance of soil temperature for external B requirements of plants is not clear. Forno *et al.* (1979) showed that in solution cultures supplied with 46 uM B, root temperatures of 23 or less ^{o}C induced B deficiency in cassava plants. The susceptibility of cassava to B deficiency was attributed partly to the effect of low temperature in depressing B absorption rates per unit root weight and in part to a decreased root: shoot ratio (Table 1). Low soil temperatures may have field significance for crop B nutrition as illustrated by the results of Rerkasem *et al.* (1989) who found that the incidence of B deficiency symptoms irrigated in black gram seedlings increased when sown in the cool season compared to warmer conditions. Since the response in blackgram was mainly in emergence, soil temperatures were believed to be more important in the plant response than air temperatures but the two were confounded as they will usually be in field experiments. However, Oertli (1962) concluded that air temperatures were more important for B uptake than root temperatures. Moreover, in maize, low soil temperature depressed plant growth and B uptake equally so that B deficiency was not induced (Lal *et al.* 1975).

Table 1. Effects of root temperature and B supply on dry matter of cassava after 40 days in nutrient solutions. Values are means of three replicates. Source: Forno *et al.* (1979)

Root temperature	B added (mg/pot)				Main effects
	0	5	15	45	
19	*3.5*	*5*	4.9	4.0	4.4
26	*8.0*	12.3	12.1	*7.5*	10.0
33	*6.3*	11.6	*8.3*	*8.3*	8.6
40	*0.8*	2.6	3.1	2.2	2.2
Main effects	4.7	7.9	7.1	5.5	

Values in shading denote plants with deficiency (light shading) or toxicity (dark shading) symptoms.

3. SOIL BORON SUPPLY

Boron sorption in soils varies with pH. As pH increases, the proportion of soil solution B present as the borate ions increases whereas the proportion of positively charged sites on variable charge surfaces decreases (Barrow 1985). The net consequence of these two opposing processes is that B sorption generally increases with increasing pH above 6.5 and peaks at pH 8-9. Consequently, critical soil B levels for crop growth are typically higher in alkaline soils than in acid soils.

Soil analysis has proved reasonably successful in predicting B response in plants (Morghan and Mascagni 1991), although not universally so (Sims and Johnson 1991). Most widely used is the hot water extraction or its variants such as the hot $CaCl_2$ method now favoured in most laboratories (Shorrocks 1991). However, it is increasingly obvious that no single critical B concentration can be used to predict B deficiency: critical values will vary with the environmental factors affecting B uptake such as soil water, soil texture with soil pH (Sims and Johnson 1991; Shorrocks 1991) and with cultivars. Few studies have established relationships between extractable soil B levels and wheat yield. Rerkasem *et al.* (1988) showed that wheat yields were not depressed on a sandy loam soil at Chiang Mai when soil hot water soluble B levels were 0.15mg/kg, but on a similar soil with a hot water soluble B level of 0.12mg/kg, gram yield was depressed by 45 % (Rerkasem *et al.* 1989). By contrast, in northeast China, complete sterility of wheat was reported when soils contained 0.18 - 0.22 mg B/kg and partial sterility at 0.32 - 0.38 mg B/kg (Li *et al.* 1978).

4. CULTIVARS

Whilst cultivars of many species vary in their micronutrient efficiency, most evidence suggests that differences in efficiency are related to external requirements rather than internal requirements. The same is probably true of B although we know of no direct evidence on this point. For B toxicity, mechanisms of tolerance operate in the roots where tolerant cultivars exclude B: the tolerant cultivars do not tolerate higher B concentrations in their tissues. According to Nable *et al.* (1991), tolerance to excess B and efficiency under low soil B operates by a single mechanism located in the roots.

Brown and Jones (1971) used two tomato cultivars to demonstrate that the cultivar differences in B uptake into shoots were located in the roots rather than shoots. When grown at the same external B concentration cultivar Rutgers transported more B from roots to shoots than cultivar T3238. In an reciprocal grafting of the shoots of one cultivar to the roots of the other, they showed that it was the root system which controlled B uptake since most B was transported to shoots by plants with the rootstock of cultivar Rutgers. Hence it seems reasonable to conclude that B efficiency is due to differences in external rather than internal B requirements. In due course it would be preferable to test this point directly rather than relying on inference.

TOTAL BORON REQUIREMENTS

The higher the yield potential of a crop, the greater the total B requirement which must be supplied by the soil. It is easy to overlook the fact that total radiant energy and soil water available during the growing season, and adaptation of crop cultivars to the growing environment combine to set a yield potential. Wheat grain contains about 8 g B/tonne: to grow a wheat crop yielding 3 tonnes of grain/ha required about 60 g B/ha (Table 2). By contrast, to grow the same yield of sunflower seed would require 400 g B/ha. Consequently, it is hardly surprising that sunflower is regarded as being very sensitive to B deficiency whereas wheat is not (Martens and Westermann 1991). It follows also that wheat crops which have a yield potential of only 1.5 tonne/ha will require less B than a wheat crop which yields twice as much: thus the effectiveness of agronomic practices such as weed control, supply of other nutrients such as N which determine how much of yield potential is realized will also interact with B deficiency. Failure to attend to these factors may cause the expression or intensity of B deficiency to vary from year-to-year, and from site-to-site.

Crop demand for B will also vary during growth. If periods of rapid vegetative dry matter accumulation coincide with early reproductive growth then competition for B between vegetative sinks and reproductive sinks may induce deficiency because the rate of B supply from the soil cannot keep pace with the demand in growing tissues, especially if environmental factors either depress B uptake (eg. low soil water) or increase internal B requirements (eg. high light, low temperature).

Table 2. Boron requirement for growth and removals in harvested crop (g B/ha). Source: Shorrocks (1992b).

Crop	Yield (t/ha)	Requirement for growth (g/ha)	Removal in harvested crop (g/ha)
Medicago sativa	7	350	350
Beta vulgaris	50	480	300
Helianthus annuus	3.5	400	100
Brassica napus	4	320	80
Triticum aestivum	3	60	25

CONCLUSIONS

Boron deficiency interacts strongly with environmental factors. Whilst the mechanisms governing these interactions are poorly understood, they stem from the need for a continuous supply of B to growing tissues in the plant. Boron deficiency occurs when the rate of supply of B to growing tissues falls below the rate of demand. It can occur when demand increases as a result of increased absolute growth rate or as internal requirements increase to cope with environmental stresses. Supply may be depressed by environmental factors such as water and temperature which depress B uptake by roots. That these factors act in a dynamic rather than a static manner adds to the challenge of predicting when and where B deficiency will occur and its impact on sterility in wheat.

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